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CLAMMING UP: ENVIRONMENTAL FORCES DIMINISH THE PERCEPTIVE ABILITY OF BIVALVE PREY

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Abstract. The lethal and nonlethal impacts of predators in marine systems are often mediated via reciprocal detection of waterborne chemical signals between consumers and prey. Local flow environments can enhance or impair the chemoreception ability of consumers, but the effect of hydrodynamics on detection of predation risk by prey has not been investigated. Using clams as our model organism, we investigated two specific questions: (1) Can clams decrease their mortality by responding to predators? (2) Do fluid forces affect the ability of clams to detect approaching predators?

Previous research has documented a decrease in clam feeding (pumping) in response to a neighboring predator. We determined the benefits of this behavior to survivorship by placing clams in the field with knobbed whelk or blue crab predators caged nearby and compared mortality between these clams and clams near a cage-only control. Significantly more clams survived in areas containing a caged predator, suggesting that predator-induced alterations in feeding reduce clam mortality in the field.

We ascertained the effect of fluid forces on clam perception of predators in a laboratory flume by comparing the feeding (pumping) behavior of clams in response to crabs and whelks in flows of 3 and 11 cm/s. Clams pumped significantly less in the presence of predators, but their reaction to blue crabs diminished in the higher velocity flow, while their response to whelks remained constant in both flows. Thus, clam reactive distance to blue crabs was affected by fluid forces, but hydrodynamic effects on clam perceptive distance was predator specific. After predators were removed, clams exposed to whelks took significantly longer to resume feeding than those exposed to blue crabs.

Our results suggest that prey perception of predators can be altered by physical forces. Prey detection of predators is the underlying mechanism for trait-mediated indirect interactions (TMIIs), and recent research has documented the importance of TMIIs to community structure. Since physical forces can influence prey perception, the prevalence of TMIIs in communities may, in part, be related to the sensory ability of prey, physical forces in the environment that impact sensory performance, and the type of predator detected.

Key words: *blue crab; chemoreception; clam; flow; hydrodynamics;* Mercenaria mercenaria; *perceptual distance; predator–prey interaction; trait-mediated indirect interaction; turbulence; whelk.*

INTRODUCTION

Predators commonly have profound impacts on prey populations and on the organization and function of communities (Paine 1966, Carpenter et al. 1985, Menge 2000). Predators in marine (Estes and Palmisano 1974, Estes et al. 1998, Menge 2000), freshwater (Carpenter et al. 1985, McQueen et al. 1989), and terrestrial (Schmitz et al. 1997, Schmitz 1998) environments affect communities through lethal predation (Sih et al. 1985), and by nonlethal mechanisms in which consumers alter characteristics of prey such as behavior or morphology (Turner and Mittlebach 1990, Katz and Dill 1998, Nakaoka 2000). These and many other studies indicate that interactions between predators and prey alter patterns of energy flow, community diversity and composition, and the importance of competitive interactions.

Studies examining the impact of predators on communities traditionally have focused on lethal effects (Sih et al. 1985) and have led to important conceptual developments such as the trophic cascade (Carpenter et al. 1985). Current studies have shown that nonlethal effects of predators can affect communities in ways that rival or mimic effects stemming from prey consumption, such as by generating trophic cascades through changes in prey behavior (Turner and Mittlebach 1990, Schmitz et al. 1997, Trussell et al. 2003). Indirect effects of predators such as those previously described are termed "trait-mediated indirect interactions" (TMIIs, Abrams et al. 1996).

Although predation is a strong community structuring force in many areas, the effect of predators is often minimal in habitats that experience substantial physical stress (Menge 1976, Menge and Sutherland 1987). Predators in these systems are unable to forage, and

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communities consist of organisms that can withstand constant disturbance (Menge 1976, 2000). Such examples provide a clear demonstration of the important role physical forces play in structuring communities by limiting predator mobility or foraging activity. Recent research, however, suggests that physical forces may affect communities in less obvious ways. In these instances, physical forces diminish the ability of consumers to locate prey and reduce predation intensity in communities (Weissburg and Zimmer-Faust 1993, Leonard et al. 1998).

Predator–prey interactions in marine systems are often chemically mediated. Several studies have shown that hydrodynamics influence the structure of waterborne chemical plumes, as well as the perception of chemical signals by consumers (Weissburg and Zimmer-Faust 1993, Finelli et al. 2000, Webster and Weissburg 2001, Weissburg et al. 2002, 2003). For example, the ability of blue crabs to locate prey by chemoreception decreases as turbulence increases (Weissburg and Zimmer-Faust 1993), but knobbed whelks successfully follow odor plumes in more turbulent flow conditions than do blue crabs (Powers and Kittinger 2002, Ferner and Weissburg 2005).

Bivalves also use chemical signals and alter their morphology (Leonard et al. 1999) or behavior (Côté and Jelnikar 1999) after detecting chemicals emanating from predators or injured conspecifics (Katz and Dill 1998). In particular, clams reduce pumping in response to chemical cues from predators or crushed conspecifics (Smee and Weissburg 2006). Although studies have examined the impact of physical forces (e.g., hydrodynamics) on predator perceptual abilities, the effects of physical forces on the sensory ability of prey have not been studied. The lack of research on the effects of environmental factors on prey perception is surprising given that studies of predator-induced prey behavior and risk assessment are commonplace (Lima and Dill 1990, Katz and Dill 1998), and that changes in olfactory-mediated prey behavior can significantly impact communities (Turner and Mittlebach 1990, Schmitz et al. 1997, Trussell et al. 2003, Werner and Peacor 2003). In addition, recent studies indicate prey responses to danger may vary across spatial and temporal scales (Lima 1998, Lima and Bednekoff 1999, Rohr et al. 2003, Turner and Montgomery 2003).

Since physical forces can alter the perceptive ability of consumers, we hypothesized that environmental forces might affect prey perception and alter the spatial and temporal scales at which prey perceive threats. In this study, we examined the impact of hydrodynamic forces on the ability of hard clams, *Mercenaria mercenaria*, to detect blue crab and knobbed whelk predators. This system was selected due to the ecological importance of these predator–prey interactions (e.g., Micheli 1995, 1997, Nakaoka 2000), prior knowledge regarding sensory biology of blue crab and knobbed whelk predators (e.g., Weissburg and Zimmer-Faust 1993, Powers and Kittinger 2002, Weissburg et al. 2002, Ferner and Weissburg 2005), and because previous work has shown that flow environments can affect the perceptive ability of predators and change predation intensity in natural systems (Weissburg and Zimmer-Faust 1993, Leonard et al. 1998, Moore and Grills 1999, Finelli et al. 2000, Webster and Weissburg 2001, Ferner and Weissburg 2005). In particular, we hoped to complement the existing understanding of how hydrodynamics affect predator ability with a similar analysis of its effects on prey. Understanding both predator and prey sensory abilities may ultimately lead to an appreciation for how the physical environment affects predatory interactions. We asked two specific questions in order to further this goal: (1) Do clam responses to predators increase their survival in natural habitats? (2) How do physical forces affect the ability of clams to detect predators from a distance? Our results suggest that physical forces alter the sensory ability of prey and may influence the prevalence of both lethal and nonlethal predator effects in communities.

Methods and Materials

Animal capture and maintenance

Animals used in this study were collected from Wassaw Sound, Georgia, USA, and associated tributaries. Hard clams, *Mercenaria mercenaria,* were dug from intertidal habitats, and knobbed whelks, *Busycon carica,* were collected from intertidal mudflats. Blue crabs, *Callinectes sapidus,* were collected in the Skidaway, Wilmington, and Herb Rivers using crab pots. Animals were returned to the Skidaway Institute of Oceanography (SkIO) near Savannah, Georgia and housed in flow-through sea tables supplied by water pumped from the Skidaway River and filtered through both gravel and sand filters. Water temperature and salinity in the sea tables ranged from 25° to 30°C and from 29 to 32 g/kg of marine salts, respectively. Clams were allowed to acclimate for at least 6 hours prior to behavioral assays and were not used in behavioral experiments if they had remained in the sea tables for longer than 48 hours. Knobbed whelks and blue crabs were fed an ad libitum diet of clams for at least one week prior to use in the field experiment or behavioral assays. Each crab, clam, or whelk was used once and then returned to the field.

Effects of clam behavioral changes on mortality

Previous research has shown that clams reduce their feeding time after detecting predators (Irlandi and Peterson 1991, Smee and Weissburg 2006) and grow more slowly in the presence of consumers (Nakaoka 2000). Presumably, these feeding reductions reduce the amount of attractive chemicals clams liberate into the environment and decrease their apparency to consumers. We used a simple field experiment to determine if predator-induced changes in clam behavior increase clam survival in natural environments. These experi-

ments consisted of establishing clam plots in the field and determining whether clam survivorship increased when predators were placed in close proximity to clams but incapable of directly interacting with them. The objective of this experiment was to alter clam feeding rates in response to predators and measure subsequent changes in clam mortality.

Clam plots contained 15 clams, 10 juveniles (shell size <30 mm) and 5 adults (shell size >35 mm), in a 0.25-m^2 area (0.5 m $\times$ 0.5 m), and this density mimics naturally occurring populations in the study area (Walker 1987). Clams were individually tethered with monofilament line (15 cm long) glued to the shell and tied to ropes strung between two lengths of polyvinyl chloride (PVC) pipe (50 cm long $\times$ 1.25 cm in diameter). Three ropes were spaced at equidistant intervals along the PVC pipe with 5 clams tethered per rope. This rope–PVC frame allowed for easy transportation of clams to the field site and facilitated the eventual sampling of clam mortality by allowing us to recover both live clams and shells of clams that were eaten.

These experiments were performed in Herb River, a tributary of the Wilmington River, which is one of two main rivers flowing into Wassaw Sound, Georgia (see Plate 1). Herb River is tidally driven, with little freshwater input beyond runoff, an average salinity of 20–26 g/kg of marine salts, a tidal range of 2–3 m, and bedded with mostly fine-grain mud. Wave action in Herb River is nearly non-existent except during periods of severe weather. Potential clam predators were identified using commercially purchased crab traps baited with either fish (to attract blue crabs) or with live clams (to attract knobbed whelks, as they rarely recruit to traps baited with carrion; M. C. Ferner, *unpublished observation*). We placed 20 pairs of traps in our field site for 48-hour periods from July to November 2003. Clam and fish-baited traps caught an average of $\sim$1 (range 0–5) and $\sim$4 (range 0–13) crabs, respectively. Although we commonly catch knobbed whelks in other areas using these trapping methods, we did not catch any whelks in Herb River. Additionally, whelks leave distinctive marks on bivalves (Micheli 1997, Nakaoka 2000), and clams recovered from our clam plots did not show evidence of whelk predation.

Plots were placed in the field in groups consisting of three predator treatments. Within each group, plots were $\sim$5 m apart, and groups of three were spaced $\geq$100 m apart. The treatments consisted of crab or whelk predators and no-predator controls. Predators were placed individually in vexar mesh cages (0.30 m diameter $\times$ 0.30 m tall, mesh size 1.0 cm^2) anchored to PVC poles pushed into the sediment, and a 0.9-kg weight was placed in each cage to hold it firmly on the substrate. The cage perimeter was $\sim$35 cm from the center of the plot, and cages were placed on either side of the plot along the predominant current direction to insure that clams were always downstream of predators regardless of tidal flow direction. Controls were alike in every way, except cages did not contain predators. Clam plots were placed in the intertidal zone ($\sim$0.0 to +0.15 m relative to mean low water) at low tide from August to October 2003, and all plots in each grouping of three were placed at the same tidal height. Clam plots were recovered after 48 hours in the field, and the number of clams recovered alive in each plot recorded. The number of surviving clams in each plot type (crab, whelk, or control) was compared using a single-factor ANOVA (Sokal and Rohlf 1995).

PLATE 1. Author D. L. Smee placing clam plots on an intertidal mud flat, Herb River, Georgia, USA. Photo credit: Matthew C. Ferner.

We established predator exclusion plots early during our studies to assess clam survivorship and recovery in the absence of predation. These exclusion plots were constructed using the methods just described, but one member of each pair was covered by vexar mesh to exclude predators while the other was left uncovered (control). Plots were placed in the field in pairs ($n = 10$ pairs). All of the clams were recovered from the exclusion plots alive, while almost 60% of the clams in the uncovered plots were crushed by crab predators or missing. Thus, we counted both empty shells and clams missing from experimental plots as having been eaten by crabs. Other investigators have followed a similar logic (Micheli 1997, Nakaoka 2000).

TABLE 1. Summary of hydrodynamic parameters for flow regimes used.

Location in flume	u (cm/s)	u^* (cm/s)	RMS (turbulence)	Re*
1.0 m upstream from clam bed	3	0.22	0.38	2.1
Over clam bed	3	0.18	0.42	1.7
1.0 m upstream from clam bed	11	0.57	1.21	5.2
Over clam bed	11	0.63	1.32	5.8

Note: Variables are as follows: u, free-stream velocity; u^*, shear velocity; RMS, the root mean square of fluctuations over the velocity time series measurements; and Re*, roughness Reynolds number. Flow conditions were measured 1.0 m upstream from the clam bed and directly over the clam bed to insure that flow conditions were generally uniform throughout the working area of the flume.

Hydrodynamic environment

The flume.—Clam behavioral assays were conducted in a paddle-driven racetrack flume at SkIO (4.8 m long working section × 1 m wide × 0.33 m water depth). This flume produces stable and reproducible boundary layers at current speeds ranging from 1 to 15 cm/s. See Ferner and Weissburg (2005) and Smee and Weissburg (2006) for a more detailed flume description and characterization of the flow environment.

Hydrodynamic methods.—Shear velocity (u^*), roughness Reynolds number (Re*), and the degree of turbulent velocity fluctuations are useful measurements of benthic boundary layer flows, and are frequently used to characterize odor plume structure (e.g., Denny 1988, Weissburg and Zimmer-Faust 1993, 1994, Weissburg 2000). Flow velocities in the flume were measured with an acoustic Doppler velocimeter (ADV; SonTek Micro-ADV field probe; San Diego, California, USA) and vendor-supplied software. ADV measurements were made at 15 heights within the log layer region of the boundary layer (i.e., the first 30%, or 10 cm extending from the substrate), and a free-stream ADV measurement was made at 15 cm above the substratum. Each height was sampled for 5 min at a frequency of 10 Hz.

Shear velocity (u^*) is a measure of momentum transfer in the boundary layer and is related to the strength of velocity fluctuations (turbulence) near the substrate (Schlichting 1987, Denny 1988, Weissburg 2000). Shear velocity was calculated by regression fit using the Karman-Prandtl equation ("law of the wall") from the ADV data collected at different heights (Schlichting 1987, Denny 1988). All regressions used to calculate shear velocities had $r^2 = 0.95$.

Turbulence was determined by calculating the root mean square (RMS) of velocity fluctuations over the 5-min velocity time series measured with the ADV 0.05 m above the substrate. This height was selected because it is within the region sampled by blue crab and knobbed whelk olfactory appendages.

Roughness Reynolds Number (Re*) is a coarse fluid calculation that provides an estimation of turbulent eddy penetration into the boundary layer in nonrippled substrates. This "rule-of-thumb" parameter is less precise than measurements of u^* or RMS, but may nonetheless convey a reasonable intuitive sense of the flow environment. Roughness begins to affect the boundary layer at $3.5 < \text{Re}^* < 6$, and boundary layers are considered fully rough at $75 < \text{Re}^* < 100$ (Schlichting 1987, Denny 1988, Weissburg 2000). Roughness Reynolds Number was calculated by

$$\text{Re}^* = (u^* D)/\nu$$

where u^* is the shear velocity, D is the hydraulic roughness length (the diameter of grains forming the bed in nonrippled substrates), and ν is the kinematic viscosity of the fluid. Mean sand grain size was 0.11 cm in our assays.

We measured and calculated free-stream velocity (u), shear velocity (u^*), RMS, and Re* at two locations in the flume: over the clam bed and 1.0 m upstream from the clam bed, to insure that the flow was relatively uniform throughout our experimental area (Table 1).

We also measured flow in the field to insure that flume flows were similar to those in our field site. We continuously recorded flow velocity at 10 Hz during a full tidal cycle, with the ADV measuring velocity 0.05 m above the substrate and placed 0.15 m above the mean low water line. Flow velocity ranged from 0.1 cm/s to 15 cm/s and RMS ranged from 0.3 to 7.7. Flow properties used in the flume experiments were within the range of those measured in our field site (Table 1) and mimic flows used in other flume studies with blue crabs and knobbed whelks (Weissburg and Zimmer-Faust 1993, 1994, Weissburg et al. 2002, Ferner and Weissburg 2005).

Behavioral assays

General methods.—Our experiments utilized changes in clam pumping behavior as assays for the ability of clams to detect predation risk. Although previous investigators have assumed that clams are actively pumping only when their siphons are extended (e.g., Irlandi and Peterson 1991), we performed preliminary experiments to verify this supposition. We visualized the excurrent from clams by carefully pipetting a 0.1% solution of fluorescein dye above the excurrent siphon of a clam. Thirty-six clams that had their siphons extended were tested in this manner, and all were releasing an excurrent. We tested 15 clams with open shells but withdrawn siphons, and only three were pumping. Thus, we concluded that siphon extension was indicative of pumping.

In each trial, five clams were placed in the false bottom of the flume and were allowed to acclimate for 30 min. Clam density in these experiments was 5 clams/0.07 m^2 and mimics densities observed in natural habitats (Walker 1987; D. L. Smee and M. J. Weissburg,

unpublished data). Predators were introduced at the conclusion of the acclimation period. We recorded the siphon position of each clam (extended or not) prior to introduction of the predator treatments and then at 5-min intervals for 30 min. Thus, each clam could have been observed pumping seven times (once prior to predator introduction and six in the presence of the predator), and the number of observations in which clams were pumping was our measure of pumping time (i.e., the response of each clam was characterized by a single value from 0 to 7).

The burrowing depth of each clam was measured with calipers at the conclusion of the experiment. Clam burrowing depth results are not presented because they were highly variable and presented no evidence of a significant treatment effect.

The order of treatments and controls in these experiments was randomly assigned each day, and behavioral assays with each treatment and the control were replicated at least five times (5 trials $\times$ 5 clams per trial $=$ 25 clams for each treatment and control). To insure independence, each clam and predator was used only once. Clams that neither pumped nor burrowed during the acclimation period were excluded from analysis, and we excluded ~25% of the clams from the experiment using this criterion.

Effects of flow on clam responses to predators.—Flow environment and distance from chemical sources affect predator chemoreception ability (e.g., Weissburg and Zimmer-Faust 1993, 1994, Powers and Kittinger 2002). To evaluate the effects of hydrodynamics on prey perception, we conducted behavioral experiments at two flow speeds (3 cm/s, 11 cm/s) and placed blue crab or knobbed whelk predators 0.5 m or 1.0 m upstream from the clams. These flow velocities were selected because they were within the range of those measured in our field site.

Duration of predator effects on clam pumping.—We measured the duration of time that clam pumping was affected by predators by removing predators at the conclusion of the 30-min behavioral assay and measuring the amount of time needed for clams to resume pumping. Clam pumping was monitored 5 min after predator removal and again after an additional 25 min. In this experiment, predators were placed 0.5 m upstream from the clams in a flow of 3 cm/s.

Data analysis.—We define a flow condition as an experiment conducted at one particular flow velocity with treatments placed at a fixed distance (0.5 or 1.0 m) upstream. We performed behavioral assays in four separate flow conditions: (1) 3 cm/s flow velocity with predators placed 0.5 m upstream, (2) 3 cm/s flow velocity with predators placed 1.0 m upstream, (3) 11 cm/s flow velocity with predators placed 0.5 m upstream, and (4) 11 cm/s flow velocity with predators placed 1.0 m upstream. Separate trials were performed within each flow condition. Each trial involved measuring feeding responses of a group of five clams in the presence of a whelk, crab, or in a no-predator control. We completed at least five trials (5 clams $\times$ 5 trials $=$ 25 clams) for each treatment (whelk, crab, or control) in each flow condition.

In our behavioral experiments, the pumping activity of each clam was monitored in the presence of either an individual blue crab, or knobbed whelk, or in a control without predators. Previous research has shown that adjacent clams behave independently of one another (Smee and Weissburg 2006), so that these results are not biased by interactions between neighbors.

Replicate trials were used to collect data on clam responses, so we employed a nested ANOVA to determine if responses of clams in groups were significantly different across replicates of the same treatment in a given flow condition (i.e., an effect of the nest; Sokal and Rohlf [1995]). Observations of clam pumping behavior (number of siphon extensions observed for each clam) were arcsine transformed to meet ANOVA assumptions (Sokal and Rohlf 1995). The nested ANOVA did not detect a significant nest effect (all $P > 0.2$). Thus, we lumped trials within treatments, and tested the significance of the main effect using the pooled error variance (Sokal and Rohlf 1995). A Tukey-Kramer post hoc analysis was employed to test for pairwise differences between treatments (Sokal and Rohlf 1995) where necessary. Experiments examining clam responses to predators in differing flow conditions were not interspersed and were conducted at different times over a period of several months. To insure that temporal changes in clam behavior were not affecting our results, we performed control trials for each flow condition interspersed between predator treatments and compared changes in clam behavior to these corresponding controls.

Our results suggested that flow velocity and predator distance affected clam responses, and we examined these effects on clam reactions to predators using a two-way ANOVA. To reduce residual variation in clam behavior between flow conditions, we normalized the number of clam pumping observations by dividing the number of pumping observations of each clam in the presence of a crab or whelk by the mean number of pumping observations of clams in corresponding controls. We then ran separate two-way ANOVAs for clams exposed to either blue crabs or knobbed whelks and examined the effects of flow speed and distance on clam reactions to these predators.

The duration of predator effects on clam pumping was analyzed with a repeated-measures ANOVA (Sokal and Rohlf 1995). For this test, we compared the percentages of clams with their siphons extended in each group before predators were added, while predators were in the flume, and after predators were removed. We used the repeated-measures ANOVA to detect the effects of predator type, time, and an interaction of these factors on clam pumping.

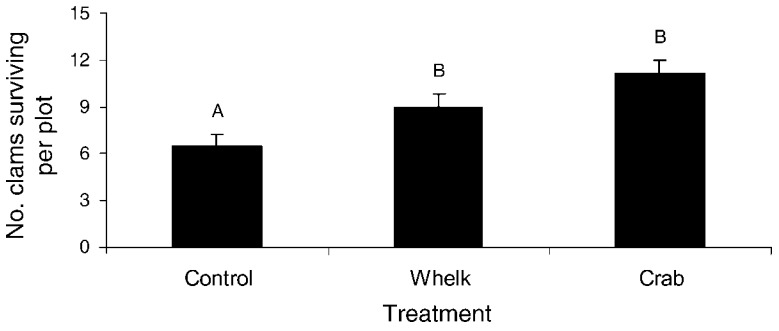

FIG. 1. Number of clams surviving per field plot (mean + SE) in the presence and absence of predators. Initial clam density was 15 clams per plot. Sample sizes were 19 no-predator controls, 16 whelk treatments, and 15 crab treatments. Different letters denote means that are significantly different, based upon a Tukey-Kramer post hoc test, and reveal that both caged crabs and whelks increased clam survival in the field.

RESULTS

Results from the field experiment

Clam survivorship increased when predators were caged next to potential prey but not allowed to interact directly with them (Fig. 1; $F_{2,47} = 9.17$, $P < 0.001$). Survivorship was 37% to ~75% higher in whelk and crab treatments, respectively, relative to survival in the no-predator controls. These values correspond to survivorships ranging from <50% in controls to nearly 80% in the crab treatment. Clam predators leave distinctive marks on clam shells (Micheli 1997, Nakaoka 2000), and we determined that all clams eaten in the experiment were consumed by crabs.

Characterization of flow regimes in the behavioral trials

The flow velocities used in our flume experiments were within the range of those measured in the field (Table 1). Vertical velocity profiles indicated turbulent boundary layers in the flume, and u^*, turbulence magnitude (RMS), and Re* at the most upstream predator location (1 m) were similar to those occurring in the middle of the clam bed, suggesting that our experimental arena was relatively free of flow artifacts. As expected, u^*, RMS, and Re* increased with flow velocity (Table 1).

Behavioral assays

Clam responses to predators.—Clams reacted to the presence of blue crabs and knobbed whelks by

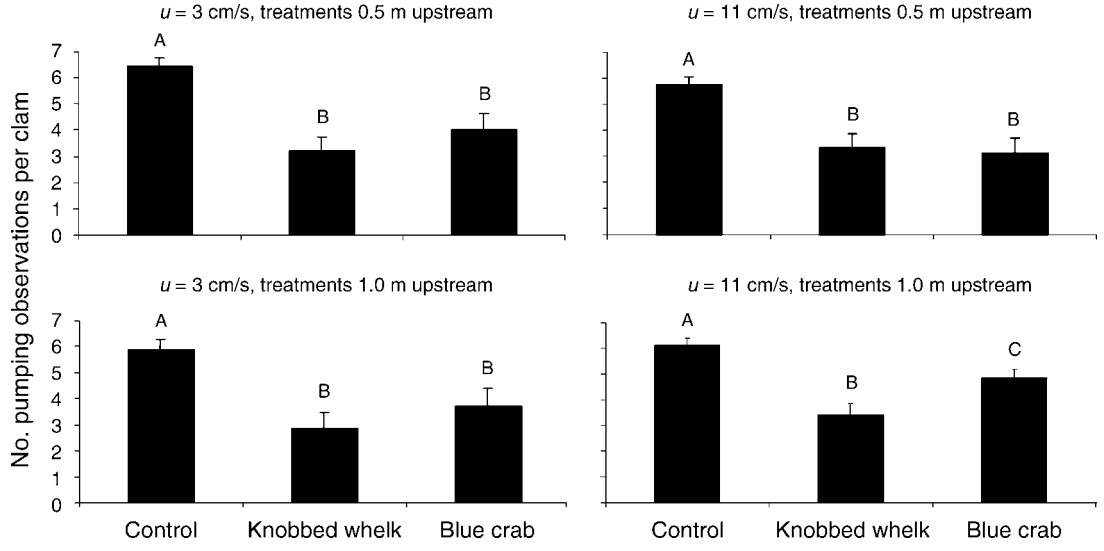

FIG. 2. Number of pumping observations per clam (mean + SE) with treatments (control and predator addition) at 0.5 m and 1.0 m upstream in two flow regimes ($u = 3$ cm/s and $u = 11$ cm/s over sand). Different letters denote means that are significantly different based upon a Tukey-Kramer post hoc test. At an upstream distance of 0.5 m, sample sizes consisted of 17, 20, 17 clams at 3 cm/s, and 23, 21, 16 clams at 11 cm/s for control, whelk, and crab treatments, respectively. At an upstream distance of 1.0 m, sample sizes consisted of 38, 37, 38 clams at 3 cm/s, and 38, 41, 35 clams at 11 cm/s for control, whelk, and crab treatments. Different sample sizes result from exclusion of inactive clams from analyses. Each clam could have been pumping seven times during the 30-min observation period.

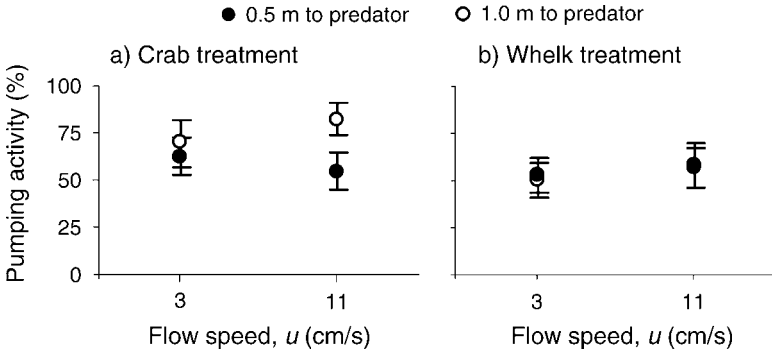

FIG. 3. Effects of flow speed and predator distance upstream on clam pumping. Circles represent pumping activity, the percentage of pumping observations per clam observed in the presence of (a) crabs and (b) whelks (mean ± SE). Clam pumping was standardized between flow conditions by dividing the number of observations in which clams were pumping by the mean number of pumping observations in corresponding controls. Thus, clams in experimental treatments that were observed to pump the same number of times as the control were assigned a value of 1. Clams responded similarly to blue crabs regardless of upstream distance when $u = 3$ cm/s, but clams showed a greater decrease in pumping when crabs were 0.5 m upstream than when they were 1.0 m upstream when $u = 11$ cm/s. Clams responded similarly to whelks in all tested flow conditions. Therefore, clam reactive distance to blue crabs is affected by an interaction between flow speed and distance upstream.

significantly reducing their feeding time ~20–50% relative to no-predator controls (Fig. 2). When $u = 3$ cm/s, clams pumped significantly less in the presence of knobbed whelks and blue crabs placed 0.5 m ($F_{2,51} = 9.69$, $P < 0.005$) and 1.0 m ($F_{2,110} = 23.22$, $P < 0.005$) upstream (Fig. 2). Similarly, at $u = 11$ cm/s, clam pumping was significantly less in the presence of predators placed at 0.5 m ($F_{2,57} = 9.85$, $P < 0.0005$) and at 1.0 m upstream ($F_{2,111} = 17.37$, $P < 0.005$; Fig. 2). Clams reduced their feeding time by ~20% in the presence of blue crabs placed 1.0 m upstream in the 11 cm/s flow, but responded to blue crabs with a ~40% feeding reduction in all other flow conditions. Clam pumping was ~50% less in the presence of whelks in all flume experiments. Post hoc analysis revealed that clam reactions to knobbed whelks and blue crabs were significantly different from each other only when these predators were placed 1.0 m upstream in the 11 cm/s flow. Clam responses to predators were similar when predators were placed 0.5 m upstream at this same flow velocity or when the flow velocity was 3 cm/s (Fig. 2).

A two-way ANOVA comparing percentages of clam pumping time in the presence of crabs in all flow conditions found a significant interactive effect between flow and distance ($P < 0.05$), but did not find a significant effect of either flow or distance separately ($P > 0.35$). This suggests that the reactive distance of clams to blue crabs diminishes in higher velocity flows (Fig. 3). That is, the effect of blue crabs on clam pumping is controlled by both the flow environment and distance upstream to the crab. Similar analysis comparing the effects of whelks on clam pumping across all tested flow conditions did not detect an effect of flow, distance, or an interaction between these factors, indicating that clam reactions to whelks are similar regardless of flow velocity or distance upstream (Fig. 3).

Duration of predator effects on clam pumping.—We determined the length of time clam pumping was affected by exposure to each predator by comparing the pumping behavior of clams during a 60-min period. During the first 30 min, clams were exposed to knobbed whelk and blue crab predators, but the predators were removed during the final 30-min observation period. In this experiment, the flow velocity was 3 cm/s, and the treatments were placed 0.5 m upstream.

Clam pumping in the predator removal experiments was significantly affected by predator treatment ($F_{2,12} = 11.25$, $P < 0.01$), time ($F_{4,9} = 16.25$, $P < 0.001$), and the time × treatment interaction ($F_{8,18} = 2.67$, $P < 0.05$; Fig. 4). Five minutes after the addition of predators, the percentage of clams pumping was less in the predator treatments when compared to controls, and the decrease in pumping lasted for 30 min until predators were removed (Fig. 4). Five minutes after predators were removed, clams exposed to whelks still showed a dramatic decrease in pumping, but clams exposed to blue crabs had resumed pumping at a rate similar to those in controls. Thirty minutes after predator removal there were no noticeable differences in clam pumping between clams exposed to crabs or whelks as compared to clams in controls. These results suggest that clams continue to respond to whelks even after the whelks have been removed, but the effects of blue crabs on clams dissipate within 5 min after crab removal.

DISCUSSION

Results from our field study indicated that clam responses to nearby predators reduce their apparency to consumers and increase their survival (Fig. 1). These results also indicated that the predator avoidance behavior of clams measured in our laboratory assays was ecologically meaningful. We found that clams in the flume reacted to both knobbed whelk and blue crab predators by reducing their feeding behavior, but distance and flow interacted to determine clam responses to blue crabs (Figs. 2 and 3). Clams responded similarly

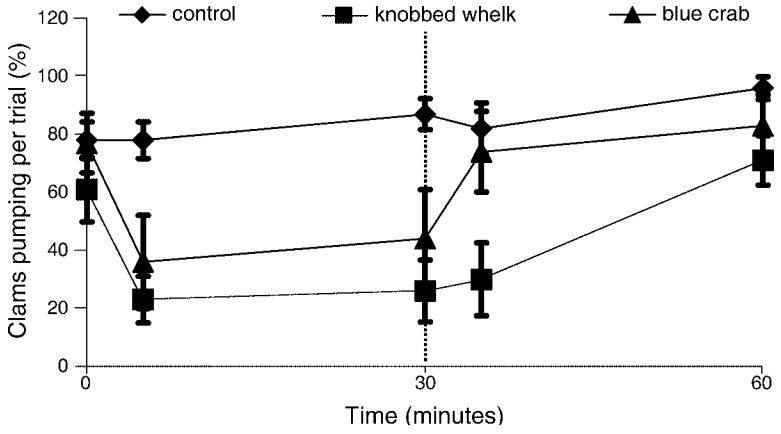

FIG. 4. Duration of time clam pumping was affected by predators. Data points represent percentage of clams pumping (mean ± SE) per trial. There were five trials for each treatment. Observations on clam pumping were made prior to addition of predators ($t = 0$), at 5 and 30 min after predator addition ($t = 5$, 30 min), and at 5 and 25 min after predator removal ($t = 35$, 60 min). The dotted line represents predator removal.

to blue crabs that were placed 0.5 and 1.0 m upstream when flow velocity was 3 cm/s. However, increasing the flow velocity to 11 cm/s resulted in a significant reduction in clam reactions to blue crabs placed 1.0 m upstream (Fig. 3). We attribute this change in clam reactions to blue crabs to a roughly threefold increase in both u^* and RMS turbulence, which are indicative of the amount of turbulence in the boundary layer (Table 1; Denny 1988, Weissburg 2000). Calculations of Re* also indicated a more turbulent boundary layer in the 11 cm/s flow. Clams responded similarly to knobbed whelks in all tested flow conditions, suggesting that the strength or quality of the chemical cue renders it highly detectable under the conditions of our trials. In addition, the duration of antipredator behavior of clams was longer in response to whelks than to blue crabs (Fig. 4).

Clam survival in the field was significantly higher in the presence of whelk and crab predators as compared to controls, indicating that clam responses to predators decrease clam mortality (Fig. 1). We attribute the increased clam survival to predator-induced reductions in clam feeding that were observed in flume experiments. The cessation of clam pumping in response to predator odors appears to make clams more cryptic to predators. These results are consistent with the findings of Nakaoka (2000), who observed that long-term exposure to caged whelks reduced clam growth rate, presumably because clams fed less in the presence of a potential threat.

An alternate explanation for our field results is that antagonistic interactions between caged and foraging predators reduced clam predation, but we feel that this is unlikely for several reasons. First, blue crabs readily approached and attempted to consume whelks in our sea tables, and blue crabs will enter crab traps baited with only live whelks (D. L. Smee and M. J. Weissburg, *unpublished data*). Thus, whelks do not inhibit crab predators, and increased survival does not result from predator interference between caged whelks and crabs. Secondly, although blue crabs are known as a bellicose species, antagonistic interactions between conspecifics seem to occur during crab feeding. Blue crabs release large quantities of prey metabolites into the water when they feed, which attracts additional crabs and often leads to aggressive interactions between competitors (Clark et al. 1999). Blue crabs housed in our sea tables often engaged in combat during feeding but rarely at other times. Recall that our caged predators could not consume potential clam prey, and thus should not interfere with ambient crab predators in our study site. Additionally, when monitoring predator density in our field site we found that multiple blue crabs commonly recruit into baited traps (~85% of our traps contained multiple animals), and Ferner et al. (2005) found that the presence of a live crab did not deter conspecifics from entering baited traps.

Previous studies indicate that fluid forces alter the structure of chemical odor plumes and change the ability of consumers to find prey (Webster and Weissburg 2001, Weissburg et al. 2002). Enhanced turbulence is detrimental to prey-finding by some predators, as shown by decreasing foraging success and efficiency when blue crabs track prey in turbulent flows (Weissburg and Zimmer-Faust 1993, Finelli et al. 2000, Weissburg et al. 2003). In contrast, knobbed whelks can successfully follow odor plumes in turbulent flows that severely diminish the perception of blue crabs (Powers and Kittinger 2002, Weissburg et al. 2002, Ferner and Weissburg 2005). Our results suggest that hydrodynamic forces may influence perceptual ability of prey as well as predators. Interestingly, differences in sensory ability of organisms suggest that an environment in which one organism is ineffective does not necessarily compromise its foe or competitor. For example, blue crabs show substantial reduction in their ability to locate bivalves in flow conditions where bivalves still can detect crabs

upstream (Weissburg and Zimmer-Faust 1993, Powers and Kittinger 2002, Weissburg et al. 2003).

Importance of prey perception to lethal predator effects

Ecologists have assumed that predators forage at optimal times or in conditions that maximize their perceptive ability (e.g., Weissburg and Zimmer-Faust 1993). This assumption has ignored both the sensory capability of prey and the effect physical forces have on sensory perception. Our results, along with others (reviewed by Weissburg et al. 2002), have clearly shown that physical forces influence sensory performance. Therefore, it is important to understand how environmental forces affect the sensory abilities of both predators and prey to appreciate how environmental forces might change the outcome of predatory interactions. We illustrate how physical forces (e.g., hydrodynamics) might simultaneously affect both predators and prey using the hypothetical case in Fig. 5. This figure is based roughly on our current understanding of blue crab–whelk–clam interactions, although further efforts are necessary to precisely characterize the relationship between perceptive ability and turbulence, and to define the turbulence levels where these effects may be important in the field as opposed to the laboratory.

Blue crabs challenged to locate dense patches of actively pumping bivalves in flumes have generally moderate success rates from distances of 0.5–1.0 m, and show a peak performance at $u^* = 0.1$ cm/s and Re* = 1.0 (Weissburg and Zimmer-Faust 1993, 1994). Blue crab prey-finding ability further declines as boundary layer turbulence increases. Successful chemical navigation is rare when crabs are 1.0–1.5 m from their prey in fully turbulent boundary layers ($u^* > 4$ cm/s, Re* > 100; J. L. Jackson, S. Rahman, M. J. Weissburg, and D. L. Webster, *unpublished manuscript*). The results presented here suggest that clam reactive distance to blue crabs also diminishes when boundary layer turbulence increases. We represent these relationships in Fig. 5, where clams initially have a sensory advantage, followed by a region of turbulence levels where predators have the upper hand, and finally, a region where high levels of turbulence diminish the perceptive ability of clams and crabs but not whelks. Whelks experience little to no decline in chemosensory perception of prey over a large range of flow conditions from nearly laminar to fully turbulent flows (Ferner and Weissburg 2005), and other slow-moving foragers are predicted to operate similarly (Weissburg 2000). Thus, whelk foraging performance is substantially unaffected by high levels of turbulence, even though turbulence erodes perception of competitors and prey (Ferner and Weissburg 2005).

These idealized relationships between predator and prey sensory performance suggest multiple and shifting outcomes of predation that depend on the physical environment. For example, environmental conditions that maximize the perceptive ability of predators may also maximize the perceptive and predator-avoidance abilities of prey, placing the predators at a disadvantage (Fig. 5). Thus, prey may thrive in areas that are ideal for foraging predators because these areas maximize their own sensory capabilities. Perhaps predators elect to forage (or are most effective) in nonoptimal conditions if those conditions are more detrimental to their prey than to themselves.

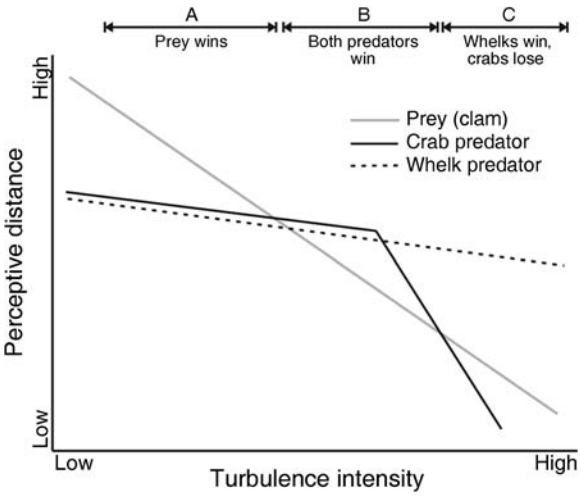

FIG. 5. Relationship of sensory ability of clams and two of their common predators: blue crabs and knobbed whelks. The figure represents idealized (linear) relationships between perceptive distance and turbulence. Future work is required to clarify the function relating perceptive distance to turbulence for these organisms, as well as identifying the precise boundaries where sensory advantages shift in the field. In Region A, both predators and prey have high perceptual ranges, but clams have a relative sensory advantage over their predators. In Region B, the relative sensory advantage shifts to predators because of an unequal rate of decline of perceptive range between predators and prey as turbulence increases. In Region C, the further decline in perception again shifts sensory advantages, but in this region, the rate of decline is less for whelks than for crabs and clams. In this scenario, a sensory refuge may exist for crab prey, although whelks are likely to be highly successful forgers. We predict that nonlethal effects of predation are high where prey have a sensory advantage (Region A), and that lethal effects predominate where predators have an advantage (Region B). In region C, predator identity becomes important, as the type of predator in this situation determines whether lethal or nonlethal effects predominate.

Joint consideration of predator and prey perception suggests that the appropriate strategy for an organism may not be to occupy areas that maximize sensory capability but instead to occupy areas that give an organism the largest sensory advantage over predators, competitors, or prey. Interactions between echolocating bats and their insect prey may be such a case. Some insects detect bat ultrasounds and respond using defensive maneuvers during flight (Surlykke 1988). To counter the insects' acoustic detection of their calls, whispering bats use a lower sound intensity that insects cannot detect, but that also reduces their perceptive distance (Dusenbery 1992).

Unfortunately, the importance of absolute vs. relative performance is difficult to evaluate, in part because environmental effects on prey perception of predation risk seem to be unknown even when constraints on predator perceptual abilities have been recognized. Some studies have identified rather coarse environmental variables, such as time of day, that affect prey evaluation of predation risk (e.g., Peckarsky 1996, McIntosh and Peckarsky 1999). However, these effects may be more related to diurnal patterns in the activity of particular predators than to specific environmental constraints on prey evaluation of predation risk. We do suggest, however, that strategies based on relative performance may be more easily identified in systems where predator and prey rely on the same sensory modality, since both participants in such a duet are likely to be affected by the same environmental features. Mutual detection of predators and prey occurs using acoustic (e.g., Surlykke 1988), visual (e.g., Blaxter 1988, Ens et al. 1993, Brown 1997, Layne et al. 1997, Skov et al. 2002) and mechanosensory (e.g., Wilcox 1988, McIntosh and Townsend 1996, Peckarsky 1996, Yen and Strickler 1996) modalities, and systems in which animals select environments to maximize their relative rather than absolute level of sensory performance may be widespread.

We define a sensory refuge as an environment in which predator perceptual abilities are insufficient to reliably detect prey before prey have the ability to engage in antipredator behavior (e.g., decreasing their apparency, initiating escape). The existence of such a refuge will depend on how each species responds to environmental forces (e.g., turbulence). Sensory refugia are more likely to exist when increasing levels of environmental forces affect predator sensory ability more than that of its prey (prey advantage) (Fig. 5). In contrast, refugia are unlikely to exist if physical forces cause greater deterioration of prey vs. predator sensory ability.

Field tests are clearly necessary to examine how turbulence impacts predation rate of prey and predators with different sensory capabilities. However, our results suggest that turbulent habitats may reduce prey perception of risk and not provide a sanctuary from consumers, as has been suggested (e.g., Weissburg and Zimmer-Faust 1993). Furthermore, the role of turbulence in altering community structure via this refuge effect (e.g., Leonard et al. 1998) remains unclear. Still, for prey that lack chemoreception, turbulent environments may well provide a refuge from consumers when these habitats negatively affect consumer chemoreceptive ability.

Importance of prey perception to nonlethal predator effects

Prey alter their behavior or morphology in the presence of predators (Katz and Dill 1998) to minimize predation risk, and predator-induced changes in prey behavior or morphology (TMIIs; Abrams et al. 1996) can have profound effects on competitive interactions and community structure (Turner and Mittlebach 1990, Schmitz et al. 1997, Schmitz 1998, Trussell et al. 2003, Werner and Peacor 2003). Predicting when and where TMIIs should occur remains an important, but elusive goal (Werner and Peacor 2003). Clearly, the impact of TMIIs will be minimal if prey cannot perceive their predators, but the role of animal perceptual abilities or limits has not received much attention when examining the role of behavioral changes in determining community structure (e.g., Werner and Peacor 2003, but see Turner and Montgomery [2003]).

Turner and Montgomery (2003) hypothesize that mobile predators moving through a habitat create a "behavioral landscape" by inducing reversible trait shifts in prey. Our results suggest the temporal and spatial grain of this landscape will vary with predator identity and environmental properties. Clam prey reduced their reaction distance for blue crabs in turbulent flows and resumed pumping quickly after brief exposure to blue crabs, but more slowly when exposed to whelks. A knobbed whelk moving through a clam bed in turbulent flow conditions would create a vastly different behavioral landscape than a blue crab. Only clams close to the crab might reduce pumping and would resume pumping shortly after the crab passes. In contrast, whelks should affect clams at greater distances and for longer times. In essence, crabs might create a highly variable landscape relative to that induced by a whelk due to the differential ability of clams to detect each consumer. The behavioral landscape might not differ when turbulence is minimal because clams appear to respond equally well to both predators under these conditions, although the effects of the whelk will linger longer after this predator has left the habitat.

In chemically mediated predator–prey interactions, areas of slow flow or reduced turbulence may allow for a greater role of TMIIs because prey are more liable to sense their predators, even though predators may sense prey efficiently as well (Fig. 5). Alternately, if reduced turbulence indeed favors the predator, then direct lethal effects should outweigh TMIIs. As before, field tests are required to resolve the ambiguity created by simultaneous shifts in perceptual ability of predators and prey with changes in flow properties. In any case, the importance of physical factors in mediating the intensity or occurrence of TMIIs is likely to be important in many aquatic systems, given the widespread occurrence of chemically mediated predator perception in these environments (Katz and Dill 1998). Indeed, the response of pulmonate snails to predator odor exhibits substantial variation that may be linked to variations in flow environment (A. M. Turner, *personal communication*), suggesting that the community-level changes stemming from predator-induced changes in snail behavior (Turner et al. 2000) may be under environmental control.

Predicting when TMIIs should be prevalent in communities, and evaluating the scales on which TMIIs occur, requires a careful examination of the environmental impacts on perceptive abilities of interacting organisms. Appropriately controlled and quantified laboratory environments may prove useful in determining the environmental conditions favoring predators vs. prey sensory systems. Although field studies are ultimately needed to document the effects of TMIIs on communities, they may be incomplete or ambiguous where heterogeneous environments that affect sensory performance have not been characterized.

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